

# MECHANISMS OF DIET SELECTION IN COYOTES (*CANIS LATRANS*)

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**ABSTRACT:** Coyote depredation is estimated to cause in excess of \$11 million in damage annually to the national livestock industry. Numerous studies suggest coyotes forage optimally. Yet, not all coyotes kill prey with high nutritional benefit to cost ratios (e.g., livestock) when given the opportunity. This suggests that there are other means by which coyotes select prey items. Little research has been conducted to determine the mechanisms driving the selection of particular food items. Previous experience with certain tastes or flavors may play a part in the subsequent selection of prey items. Dietary preferences can be formed in young animals through exposure to chemical cues in utero, in milk, and at weaning. Studies on captive animals are useful in evaluating the importance of exposure to chemical cues on the formation of dietary preferences in adult coyotes. A review of relevant literature is given and management implications are discussed.

**KEY WORDS:** coyotes, *Canis latrans*, diet selection, early experience

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## INTRODUCTION:

The coyote (*Canis latrans*) is one of the most widely studied mammals in North America primarily due to predation on domestic animals. Coyotes are generalist omnivores (Nowak and Paradiso 1983; MacCracken and Uresk 1984; MacCracken and Hansen 1987), preying upon a variety of vertebrates including small rodents (e.g., mice and voles), lagomorphs, game animals, and livestock. Coyotes also feed on fruit and vegetable crops (MacCracken 1982), which can cause increased conflict with humans. Coyote depredation is believed to cause in excess of \$1.2 million worth of damage to the Utah sheep industry each year (Anonymous 1998). Nationally, sheep and lamb losses to coyote predation accounted for over 66% of the total losses in 1994 for an estimated monetary damage of \$11.5 million (National Agricultural Statistics Service 1995).

To understand why coyotes switch from their native prey to domestic livestock and to manipulate that decision, we need to understand the mechanisms by which diet selection choices are made. A variety of diet selection models have been proposed in an attempt to answer why animals select the dietary items they do. In this paper, we will provide a brief review of the major models and discuss their potential applicability to coyote diet selection or foraging behavior.

## DIET SELECTION MODELS

According to Provenza and Balph (1990) animals have many challenges to overcome while foraging, such as the spatial and temporal variation in food quality and availability, chemical and physiological defenses, and unfamiliar foraging environments. Diet selection models are designed to predict how animals will forage in the face of these challenges. The degree to which the various diet selection models accurately predict diet choices varies considerably depending on the species. Some models explain the variation in choices made by taxonomic groups of animals well, but poorly predict individual

variation within those taxonomic groups (i.e., morphophysiology). Most of the models also do a rather poor job of providing insight into the mechanisms by which diet choices are made.

The euphagia diet-selection model suggests that animals have an innate ability to sense nutrients in their diet items. This "nutritional wisdom" allows the forager to select a nutritious diet while avoiding the ingestion of harmful substances. Animals would also be able to overcome nutritional deficiencies by selecting diet items that contain the specific nutrient that is lacking. This ability to detect a specific nutrient deficiency is more commonly known as specific hunger. However, the only specific hunger documented is for sodium (Belovsky and Jordan 1981; Beauchamp and Mason 1991). The domestic dog, however, does not form a salt appetite after sodium depletion possibly due to the fact that dogs in the wild would not experience salt depletion without first starving (Beauchamp and Mason 1991). As coyotes and domestic dogs are closely related, coyotes should not experience salt depletion in the wild either. Even though euphagia seems to describe certain behaviors, it does not accurately predict the majority of foraging behavior nor does it provide any insight into the mechanisms of these behaviors. Therefore, it has limited practical implication for managing diet selection behaviors.

Proponents of the hedyphagia model argue that animals select a nutritious diet by consuming items that are immediately pleasing to the senses. The model makes two assumptions. The first is that dietary items with unpleasing qualities are not as nutritious as those with pleasing qualities, and the second is that the same quality would be considered unpleasing to all animals. Both of these assumptions have been difficult to document. Although there have been some examples that would suggest hedyphagia was the mechanism by which animals selected diets (Arnold and Dudzinski 1978; Beauchamp and Cowart 1987), there are considerably more examples that contradict this theory (e.g., see Gustavson 1977;

Arnold and Dudzinski 1978; Fowler 1983; Garcia and Holder 1985). Some literature suggests that hedyphagia is not an important process for diet selection in coyotes. Coyotes that consume a palatable item (e.g., chicken) laced with lithium chloride will experience gastrointestinal illness and subsequently reduce their preference for that item (Gustavson et al. 1974) and no longer spend energy looking for chickens as a food source (Garcia et al. 1977). According to the hedyphagia diet selection model, the coyote should continue to eat the palatable item regardless of whether or not it experiences gastrointestinal illness. Hedyphagia, like euphagia, poorly predicts individual diet selection and provides little, if any, insight on the mechanism of diet choice.

The morphophysiology model suggests that size and physiological characteristics of the foraging animal determine the items it will select. Unlike the previous models, this model predicts diet choice well across taxonomic groups (e.g., ruminant vs. non-ruminant herbivores; carnivores vs. herbivores).

Among carnivores and omnivores, there are substantial differences in the capacities for digesting and absorbing certain nutrients. When normalized to body length or weight, the intestinal length of obligate carnivores (e.g., felines) is shorter than that of omnivores (e.g., canines); longer intestinal lengths allow for more complete absorption of nutrients (Stevens 1988). Omnivorous species (e.g., coyotes, rats, and mice) have physiological adaptations that allow them to digest a wider variety of carbohydrates and, consequently, have some capacity to adapt digestive functions to shifts in diet composition (Stevens 1988). In contrast, obligate carnivores (e.g., felines) are unable to adapt to large shifts in diet composition due to their inability to efficiently digest a variety of carbohydrates (Morris et al. 1977).

Although the morphophysiology model predicts diet choice well across taxonomic groups, it is a poor predictor of individual diet selection behavior (e.g., certain coyotes kill sheep and others do not). These shortcomings limit its applicability in wildlife management.

The learning by consequence model can accurately predict diet selection behavior on both the taxonomic and individual levels. This model states that the selection or rejection of forage items is the result of both positive and negative consequences experienced while consuming, ingesting, or digesting a prey item. There are numerous studies that indicate animals can learn to associate specific food items with negative post-ingestive consequences (e.g., Barker et al. 1977; Gustavson 1979; Ellins and Martin 1981; Ellins et al. 1983; Provenza and Balph 1988). Coyotes are capable of associating specific tastes with the ill effects of lithium chloride. Studies have demonstrated that aversions to the flavor of prey items can be established after consuming lithium chloride laced baits or carcasses (Gustavson et al. 1976). Predation studies suggest that these flavor aversions can result in the suppression of attacks on live animals (Gustavson et al. 1974; Ellins et al. 1977; Ellins and Catalano 1980), but there has been some controversy regarding the validity of these findings (Forthman Quick et al. 1985a; Lehner and

Horn 1985; Wade 1985; Ellins 1985; Burns and Connolly 1985; Booth 1985; Forthman Quick et al. 1985b).

The learning by consequence model is often accurate and provides a mechanistic explanation of why animals select certain foods. Therefore, it can provide a valuable tool for managers whose objectives are to manipulate diet selection of individuals or group of animals. However, its success depends on knowledge of the foraging history of individuals, which is often difficult to ascertain.

Optimal foraging theory is based on the assumption that animals have evolved to select a diet that maximizes their fitness. This theory predicts that food items, which provide the highest return per unit time should be selected (Stephens and Krebs 1986). It has been used extensively to predict the foraging patterns of predators including coyotes (Porter et al. 1973; Werner and Hall 1974; Porter et al. 1975; Loether 1977; Cook and Cockrell 1978; Stephens and Krebs 1986). MacCracken and Hansen (1987) determined that coyotes in southeastern Idaho foraged in a manner consistent with this theory. Coyotes in their study selected the most profitable foods available and other items were added to the diet only when the abundance of profitable foods was low. Gese et al. (1996) observed coyotes in Yellowstone National Park foraging optimally. In their study, coyotes foraged mainly in areas where detection and capture rates were highest, suggesting that these areas provide the highest net return (Gese et al. 1996). However, anecdotal observations suggest that coyotes do not always select the most profitable foods available. For example, to maximize nutrient intake per unit time, optimal foraging theory predicts that coyotes should eat foods that are easy to kill and high in nutrient content, such as sheep. However, all coyotes do not consistently kill sheep. Regardless of whether coyotes forage optimally or not, the purpose of our research is to investigate the process by which individuals select food items. Optimal foraging theory only provides the evolutionary explanation of diet selection and does not necessarily provide the process by which an animal selects a certain diet. Thus, this model does not offer any insight into the mechanism of food selection by individuals.

#### POSSIBLE DIET SELECTION MECHANISMS

Although the selection of certain dietary items is at least partially controlled by genetics, most choices are based on experience. Experience during all life stages (i.e., in utero, as a neonate, at weaning, as a juvenile, or as an adult) are important in helping an animal decide where and how to select a diet. A fetus' diet selection experience is limited to in utero exposure. After parturition, however, the neonate draws upon in utero experiences as well as those obtained while nursing. As the individual ages, its knowledge base develops through diet selection experiences. This knowledge base is analogous to a "reference library" where life stages represent the books and individual experiences are chapters in those books. The most recent volume represents the individual's current life stage, and it is this volume on which the animal relies most heavily when making diet selections. Occasionally, though, an individual may reference an earlier volume. For

example, an adult coyote may draw upon experiences gained as a juvenile when encountering a food item for which it has no recent exposure. Therefore, experiences in utero, as a neonate, or during weaning may have profound effects on the adult animal's life (e.g., Nolte et al. 1990; Nolte and Provenza 1991).

Familiarity with a flavor may be an important factor in the diet selection of many wild animals (Shumake 1977). The role of previous exposure to dietary flavors has been documented in many vertebrate species, some of which are omnivorous. During weaning, rat pups preferentially consume a diet with the same gustatory cues as that which was eaten by their lactating mother (Galef and Clark 1972; Galef and Henderson 1972; Galef and Sherry 1973). Similarly, Capretta and Rawls (1974) showed rat pups exposed to garlic through mother's milk had a higher preference for garlic than rat pups not previously exposed to garlic. Hunt et al. (1993) found rat pups exposed to ethanol in mother's milk reacted differently during testing situations, depending on the age at which they were exposed. Eight-day-old rats showed no enhanced preference for ethanol relative to controls while 12- and 16-day-old rats did have an enhanced intake. Rat pups tested during weaning were found to have an increased acceptance of caffeine in a two-bottle preference test when they were exposed to high doses of caffeine through mother's milk (Gullberg et al. 1986). Mainardi et al. (1989) found mice exposed to fennel through mother's milk ate significantly more of a fennel diet than those never exposed to fennel. Studies with piglets showed they consumed significantly more of a weaner diet when it was flavored with the same compound sows received during lactation (Madsen 1977). Distel and Provenza (1991) documented goats exposed to blackbrush twigs early in life (6 to 26 weeks of age) ate significantly more blackbrush than goats exposed only to alfalfa pellets. Similarly, Nolte et al. (1990) and Nolte and Provenza (1991) found lambs exposed to flavors early in life established lasting preferences for those flavors. Similar results were found with snapping turtles, with hatchlings exhibiting a lasting preference for an initial diet over foods which were subsequently offered (Burghardt and Hess 1966). These authors referred to this phenomenon as food imprinting.

Available evidence suggests that dogs may respond to most taste stimuli before birth. Ferrell (1984a) determined that beagle fetuses have morphologically mature taste buds at 47 days of gestation (gestation = 63 days) and are capable of responding to gustatory stimuli at that stage of development. While fetuses can respond to taste, research has yet to document the relative importance of such experiences before and after birth.

Fat-soluble flavors in the diet rapidly appear in the milk of most mammalian species when consumed by the lactating female (e.g., Moio 1996; Madsen 1977; Dougherty et al. 1962; Mennella and Beauchamp 1991). Additionally, the consumption of milk can be used as a positive reinforcer during conditioning. Stanley et al. (1963) found that neonatal shetland sheepdog and cocker spaniel puppies could be conditioned using positive (e.g., milk replacer) and negative (e.g., quinine hydrochloride) reinforcers. In all cases, the puppies exposed to the positive reinforcer treatment performed better than

puppies exposed to either the neutral or negative reinforcer treatments (Stanley et al. 1963).

Available diet selection evidence for dogs contradicts that of most other species. Ferrell (1984b) determined that early exposure (one week in utero, in milk until weaning, and first-fed solid food at weaning) to cues reflecting the mother's diet are sufficient to influence choices made by beagle puppies during weaning. Seven out of the eight litters tested in that study chose the novel-flavored food over that which was flavored with the familiar flavor. In the one case where the litter strongly preferred the familiar flavor, it was highly palatable compared to the alternative choice.

Research suggests that adult coyotes have the ability to recognize particular flavors and are capable of ranking them in a preferential order. Studies have shown coyotes place a higher hedonic value on some tastes and preferentially will consume the valued tastes (Mason and McConnell 1997). For example, sweet solutions (e.g., sucrose) are preferred to bitter solutions (e.g., quinine hydrochloride) (Mason and McConnell 1997). Research also has documented coyotes are capable of associating a flavor or taste with a negative post ingestive consequence subsequently causing an aversion (Ellins and Martin 1981; Ellins et al. 1983; Forthman Quick et al. 1985a; Gustavson 1979; Gustavson et al. 1976; Gustavson et al. 1982).

#### MANAGEMENT IMPLICATIONS

Research on diet selection mechanisms is in its infancy, and it may take years before its full potential is realized. However, some potential applications are apparent. Most animals are extremely wary of novel surroundings (Harris 1983) and tend to have a higher acceptance of familiar foods than novel ones (Shumake 1977). Exposing young animals to specific foods may increase the acceptance of those foods by adults. One possible way to achieve such exposure is through milk. For example, current research is being conducted with coyotes to determine if flavors in milk enhance the intake of similarly flavored foods later in life. If preferences are established in milk, coyotes exposed to "bait" flavors while nursing mother's milk may seek out those baits later in life, thereby increasing management success.

Another management implication is to increase the effectiveness of removal devices such as the M-44. One way to make M-44s more effective is to increase the likelihood that animals will pull them when they are placed. Research is currently being conducted to determine if pre-baiting M-44 lines with inert baits (marshmallows) will increase the likelihood that active M-44s will be pulled. The marshmallow bait is attractive to the coyote because of its sweet taste and it mimics the bait used on active M-44s. Therefore, coyotes associate the positive aspects of the marshmallow with the M-44 line. Due to the decreased neophobia toward the M-44 and the reinforcement from the marshmallow pre-baiting, coyotes should increase the pull response on active M-44s (J. R. Mason, pers. comm.).

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